Genetic Improvement of Eucalypts

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Summary

The paper emphasises the importance of knowledge of the breeding system of a eucalypt species when attempting genetic improvement of yield and other characters through selection within the best populations.

Field trials of open-pollinated families from natural populations of several eucalypt species have shown considerable genetic variation between and within populations.

Recent research on the proportion of selfing and outcrossing in eucalypts, while supporting the general predominance of outcrossing, has revealed that the proportion might differ from one eucalypt species to another, and that eucalypts have a much higher degree of selfing than pines. Therefore, in planning genetic improvement of eucalypt populations, the consequences of selfing may be a more important consideration than is the case in the improvement of pines.

Key words: Eucalyptus species, breeding systems, breeding strategy, base populations, hybrids, genetic variation, selection, seed production areas, seed orchards.

Zusammenfassung

Zur genetischen Verbesserung des Holzertrages und anderer Merkmale bei Arten der Gattung *Eucalyptus* sind folgende Besonderheiten zu berücksichtigen:

1. An Hand von Versuchen mit Nachkommenschaften aus frei abgeblühten Beständen hat sich gezeigt, daß innerhalb autochthoner Populationen sowie zwischen solchen eine beträchtliche genetische Variation gegeben ist.
2. Neueste Versuche haben gezeigt, daß Eukalyptus-Arten einen höheren Grad an Selbstbestäubung aufweisen als z. B. Kiefern-Arten.

Objectives and Silvicultural Background

The objectives of the many programs of eucalypt improvement throughout the world are to increase the yield and quality of wood from plantations grown mainly for fuel and pulpwood.

About half of all wood cut in the forests of the world is burned as domestic fuel, and each year a greater proportion of the world's firewood comes from eucalypt plantations as natural forests diminish (Earl 1975).

Eucalypt wood is easy to grow, cheap due to its fast growth on a wide range of sites, and its high density makes it a good fuel. Eucalypt wood contributes a significant proportion of the energy used in developing countries in the warmer parts of the world where eucalypts grow rapidly as a crop, up to about 40° either side of the equator. In addition to fuel, eucalypt wood from young fast-grown plantations is suitable for poles and posts, and the short fibre is excellent for many grades of paper. However, such wood is less suitable for sawn timber because of its tendency to split and other defects.

There is ample evidence of the fast growth rate of eucalypts in plantations. Small sample plots of eucalypts aged 6 to 8 years in certain favourable sites in East Africa and Brazil have grown at the rate of 90 m^3/ha/yr (personal communications from H. C. Dawkins, W. G. Dyson and I. Kissin), a dry weight yield close to the practical upper limit of 50 tonne/ha/yr for fibre crops suggested by Bevege (1976). Clearly the silviculturalist can aim for more than the 10 to 20 m^3/ha/yr commonly obtained over large areas of eucalypt plantations in temperate and tropical regions (M. R. Jacobs, pers. comm.).

Some eucalypts which are well adapted to grow in a new plantation environment have unsatisfactory stem straightness or branching which might be improved by selection. For example, *Eucalyptus camaldulensis* Dehnh. in North Africa and Israel grows fast but crookedly. Selection is being made of the straightest trees as the basis for an improved cultivar (variety) of the species. In other cases fast-growing plantations of eucalypts of good form and wood quality are severely damaged by rare frosts or droughts. Selection among the survivors of frost in southeastern U.S.A. and southern Brazil aims at new frost-resistant cultivars.

The tree breeder's contribution to obtaining higher yields is to provide selected seed or cuttings with the capacity for improved growth rate, stem and branch characteristics and wood quality from the best provenances of eucalypts. In this way silviculturalists can take advantage of the new mixture of natural and man-made environmental factors in plantations.

Base Populations for Selection

It is pertinent for tree breeders to ask what populations they are trying to improve by selection.

Many eucalypt plantations have probably been derived from very few original seed trees. For example, the successful cultivar of *Eucalyptus tereticornis* Sm. in the Congo, 12ABL, appears to have come from only one or two trees in Madagascar (Martin 1971), and the Mysore gum, another cultivar of *E. tereticornis*, is also derived mainly from one small stand in India (Pryor 1966).

It has been a common practice for commercial seed collectors to obtain seed from trees with heavy crops. Often a eucalypt tree will yield several kilograms of its tiny seeds, more than enough to meet an order from an uncritical forester planting a million trees. His future seed collections are likely to be from the extensive plantations founded on one or few Australian trees.

A large plantation based on a few original trees might not be a suitable population from which to establish a tree improvement program, since many useful alleles in the original population may not have been included in the sample taken (Namkoong 1972, p. 54). In such a case it would be wise to return to the natural stands for more seed with which to enlarge the genetic base.

Another reason for enlarging the genetic base is to avoid the likely deleterious effect of inbreeding which, as the following section suggests, may be of greater importance in eucalypts than has previously been considered.

Breeding Systems

The term breeding system is used here in the comprehensive sense of Lewis and John (1972) to cover 'all those variables (except mutation) which affect genetic relations of

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gametes that fuse' in sexual reproduction, and includes pollination biology, self compatibility and the degree and effects of inbreeding.

In a previous paper (ELDRIDGE 1976) the point was made that, if inbreeding is prevalent in eucalypts, there might be reduced genetic improvement by following the breeding methods usually prescribed for outcrossing species.

If selfing is common, plus trees grafted into a seed orchard would have limited opportunity to display the high general combining ability for which they were selected. Also, selfing would limit the number of new combinations on which future genetic gain by selection depends, whether from a seed orchard or a plantation.

These limitations can be visualised with the help of a diallel crossing pattern in which the cells for crosses have a lower proportion of the total number of progeny than the cells for selfs.

Open-pollinated progeny tests are sometimes used to assess additive genetic variance, and are usually the only means available to assess general combining ability of eucalypt plus trees. If inbreeding is prevalent an open-pollinated test inflates the estimates of additive genetic variance (NAMKOONG 1966), and does not provide a good ranking of parents for general combining ability.

One way to avoid selfing would be to make controlled pollinations for further selection, and thus make full use of additive genetic variance, which in the case of *E. grandis* HILL ex MAIDEN, was estimated by VAN WYK (1976) to be of a significant magnitude. Fifteen months after planting 99 crosses of a large diallel, when the tallest trees were over 5 m, VAN WYK found that height, diameter and volume were inherited in a non-additive as well as in an additive fashion and that heritability was low, close to 0.1. However, open-pollinated tests are more likely to be used in eucalypt breeding due to the difficulty of emasculating small flowers and the shortage of money and skilled technicians in the developing countries growing eucalypts.

Many of these difficulties with methods of improving eucalypt populations will be resolved by a better understanding of eucalypt breeding systems. It is not enough to guess that eucalypts are like conifers, or that all the eucalypts are the same; it is necessary to find out the nature of the breeding system of each species by thorough investigations in natural forests, plantations and seed orchards.

There is evidence that both inbreeding and outcrossing occur in eucalypts. PRYOR (1961) summed up early experiments on the breeding system of several species of eucalypts by saying 'there appears to be a system of preferential outcrossing. In short, in the few cases examined, selfing is found to occur, but less readily than outcrossing to other individuals'. Recent studies using larger numbers of trees support PRYOR's broad generalisation of predominant outcrossing within species of the genus *(Table 1)*. These studies also confirm PRYOR's initial observations of the occurrence of a wide range of crossing patterns within species, including the two extremes of obligate selfing caused by cleistogamy (VENKATESH *et al.* 1973) and obligate outcrossing caused by self incompatibility (PRYOR 1957) or male sterility (DAVIS 1969) or female sterility (CARR *et al.* 1971; CARR and CARR 1972).

The outstanding research of HODGSON (1974, 1976, 1977) has answered many of the questions about pollination biology, the amount of selfing, and inbreeding depression for planted *E. grandis*. His investigations were aided by the availability of numerous grafts of many clones in a seed orchard and clone bank located near his laboratory and nursery.

Table 1. — Proportion of selfing in open pollinated eucalypts estimated by seedlings markers (assuming a single recessive gene, not carried by neighbouring trees), or by seed isozymes

Species	Source	Number of trees	Proportion of seed selfed
MORPHOLOGICAL MARKERS			
Eucalyptus 'alba' (1)	Krug & Alves (1949)	9	23%
E. pilularis	Florence (1969)	1	100%
E. regnans	Eldridge (1970)	1 (2)	8 & 28%
E. grandis	Hodgson (1976)	5 (3)	10- 33% av. 30%
ISOZYMES			
E. obliqua	Brown et al. (1975)	40	24%
E. pauciflora	Phillips & Brown (1977)	60	37%

(1) probably a mixture of species with *E. urophylla* S. T. Blake predominanting.
(2) top and base of crown.
(3) in orchard conditions.

The height reached by deliberately selfed progeny of nearly all clones of *E. grandis* at 11—18 months was 8% to 40% less than that of outcrossed progeny. Moreover, selfed progeny were usually more crooked, and included about 30% of abnormal seedlings. There is therefore an opportunity to identify and control at least some of the worst effects of selfing in a *E. grandis* seed orchard by culling poorer seedlings in the nursery and by testing and rejecting the more self-fertile clones. However, this was not possible in the case in *E. regnans* F. MUELL. (ELDRIDGE 1970 and unpublished) where selfed seedlings did not differ in appearance and were not consistently smaller than outcrossed or open-pollinated seedlings up to the age of one year. Inbreeding depression was not obvious until six years after planting and even then many individuals within selfed families were vigorous and of good form.

Isozyme techniques have been introduced to the study of the breeding system of eucalypts in natural forests by A. H. D. BROWN and co-workers. They used the gene frequency of three enzyme loci to estimate the proportion of seed derived from self-pollination in open-pollinated seed of *E. obliqua* L'HÉRIT. (BROWN *et al.* 1975) and *E. pauciflora* SIEB. ex SPRENG. (PHILLIPS and BROWN 1977). They found a level of self-fertilisation so high that a breeding system of predominant self-fertility could be expected to evolve unless a factor acted strongly to prevent it, such as a selective advantage in germination, growth rate and survival of heterozygotes.

There may be important differences between species in the amount of inbreeding. The most reliable estimates (on *E. obliqua* and *E. pauciflora)* suggested that these two species had different levels of self-fertilisation, though both were high. Furthermore, the three populations in the *E. pauciflora* study also had different levels of self-fertilisation: the population growing at the highest elevation had a significantly higher level of inbreeding than the other two populations.

Another aspect of the differences between species in the proportion of selfing and outcrossing, not evident from previous publications on eucalypts, arises from consideration of the data in *Table 2.*

Table 2. — Comparison of average numbers of viable seed set from controlled selfing and crossing in *Eucalyptus grandis* (HODGSON 1975), *E. regnans* (ELDRIDGE 1970) and preliminary work on *E. urophylla* by C. P. BORGES (pers. comm.). The number of trees tested is showed in brackets. The relative yield (S/X) was calculated from the seed set after selfing and crossing for 11 trees of *E. grandis* and 3 trees of *E. regnans*

	E. grandis	E. regnans	E. urophylla(1)
Proportion of trees capable of selfing	44/45	13/14	
Seeds per capsule			
Self (S)	4.6 (39)	2.5 (13)	2.5
Cross (X)	32.2 (11)	4.0 (3)	2.8
Relative yield (S/X)	20% (11)	103%(3)	
Open-pollinated	8.3	3.6	6.2

(1) possibly not pure *E. urophylla*.

In *E. grandis* many times more seed were set after crossing than after selfing or open pollination, whereas in *E. regnans* the seed set after crossing was little more than after selfing or open pollination in numbers of seed per capsule. The relative yields in *E. urophylla* S. T. BLAKE (see also GUIMARAES and KERR 1959) appear to be similar to *E. regnans*. Differences in technique (hand selfing in *E. grandis* and the help of blow flies for selfing *E. regnans* and bees for *E. urophylla*) are unlikely to account for the large differences in seed set.

The observed rates of inbreeding in eucalypts are different from those in the better-known pines. In the intensively studied members of the family Pinaceae, self-fertilisation is only 5 to 10%, abortion of selfed zygotes is 90% due to a high genetic load of embryonic lethals, and selfed seedlings suffer severe inbreeding depression (HADDERS and KOSKI 1975). In other words selfing is self-destructive in many conifers. By contrast selfing in the eucalypts examined so far is between 20% and 40% and there are indications that selfed zygotes and seedlings of eucalypts have higher chances of survival than those of conifers. It is no doubt appropriate for those conifers in which selfing is self-destructive to assume that the effects of selfing are negligible when predicting genetic gain in recurrent selection using seed orchards and open-pollinated tests (BURDON and SHELBOURNE 1971). However, because selfs appear to be more viable in eucalypts the effects of selfing should not be ignored in the genetic improvement of eucalypts.

Interspecific Hybrids

Many species of eucalypt hybridise in nature or can be crossed readily. While the interest in hybrids has been enhanced by their great value in resolving some taxonomic problems (PRYOR 1976), and by the spectacular growth of certain individuals, the large scale use of eucalypt hybrids for plantations has been handicapped for want of methods of mass production. Mass production of F_1 or other hybrids might be achieved either by a cheap means of controlled pollination, which is not yet available, or by vegetative reproduction of hybrids. Cheap methods of vegetative reproduction, though not yet widely used, have been developed to a pilot scale by CHAPERON (1977) and CAMPINHOS and IKEMORI (1977) in tropical areas. Without cheap mass production the role of inter-specific hybrids in population improvement of eucalypts is at best a curiosity and in many cases a handicap.

In many countries spontaneous hybrids which were attractive as F_1 have fallen into disuse after several rotations due to segregation (PRYOR 1976). Brazilian foresters have tried for decades to remove unwanted hybrids from their heterogeneous planting stock (KRUG and ALVES 1949). Removing unwanted hybrids might be the explanation of the successful reduction in the tendency for wood of *E. grandis* to split after four generations of selection in South Africa (ANDREWS 1961; NEL 1965). This selection could well be a case of purifying a segregating hybrid swarm of *E. grandis* and *E. saligna* rather than employing the additive genetic variation in a single species (MARSH and HAIGH 1963).

Inbred crops which have lost the capacity for improvement by selection may need an influx of new variation by hybridisation. However, natural eucalypt forests still contain rich stores of unused genetic variation (EVANS 1976). Therefore, most eucalypt breeders do not need interspecific hybridisation at present to increase genetic variation.

Provenance Trials and Seed Production Areas

Provenance trials which indicate the best geographic source of seed do not themselves provide the best seed for large-scale afforestation. Seed from the best plots in a trial will be seriously contaminated with pollen from inferior provenances or even other species. Often it is too expensive or impossible to obtain large quantities of seed from natural stands of the best provenance. In such circumstances it is necessary for the forester to take steps to grow his own seed. There are three main methods of growing eucalypt seed: (i) Seed may be collected from the first *plantations* of the chosen provenance, although in many species there is a very poor crop from dense young stands. (ii) Alternatively a *seed production area* can be established by heavy early thinning in a suitable stand of the chosen provenance. This method is cheap and quickly provides valuable seed. (iii) An expensive *seed orchard* program to obtain seed of the best possible genetic quality might be justified where the plantation scheme is large and well organised.

In any case, seed production areas could fill the gap between selection of a suitable provenance, and production from a seed orchard. However, one must be aware of the narrow genetic base and probable inbreeding among progeny of too few closely related Australian parent trees. The problems which may arise can best be explained by an example.

E. camaldulensis in the tropical savanna of northern Nigeria was an unattractive species while the unsuitable provenances from southern Australia were being grown. Recently the Petford and Katherine provenances (S.6953 and S.6869) from northern Australia were shown to be far superior to southern provenances in a series of excellent trials of 16 provenances in Nigeria (JACKSON and OJO 1973) and other places (LACAZE 1977). Some small stands raised from the original Petford and Katherine seed lots have now been thinned as seed production areas. But those collections represent only five female parents at Petford and ten at Katherine and an unknown number of male parents. Furthermore, the amount of seed collected per tree varied widely. These numbers were adequate for provenance trials but dangerously few to be the genetic base of a breeding program to supply seed for thousands of hectares of much-needed plantations. Until we have much more knowledge of the consequences of inbreeding in *E. camaldulensis*, a safer genetic base for northern Nigerian plantations would be new collections near Petford and Katherine from 50 or more widely separated large trees of good form.

Selection and Seed Orchards

Effective improvement by selection within a population depends on the presence of sufficient additive genetic variation. Good estimates of genetic parameters (especially additive and non-additive genetic variance, phenotypic and genetic correlation between characters selected, and coefficient of inbreeding) are needed to predict gain from alternative strategies for genetic improvement and to choose the best strategy. Eucalypt improvement programs were well advanced before the first reliable estimates of genetic parameters were made by VAN WYK (1975). His estimates were based on 15-month-old progeny of a 15 × 15 partial diallel of outstanding phenotypes of *E. grandis.* He found useful amounts of both additive and non-additive genetic variance in several characters. Recent studies of progeny from natural stands of *E. obliqua* (BROWN *et al.* 1976), *E. regnans* (ELDRIDGE 1972) and *E. nitens* (DEANE & MAID.) MAID. (PEDERICK 1976) have shown ample genetic variation *within* populations for selection for growth rate and other characters.

Since estimates of heritability are low in eucalypts (ELDRIDGE 1972; VAN WYK 1976), more genetic improvement would be obtained by family selection than by individual selection. This is because parental genotypes are identified more reliably by selecting the best families in progeny tests than by selecting outstanding phenotypes ('plus trees') in the forest.

Harnessing the additive genetic variation within well adapted populations or provenances of eucalypts has been undertaken through clonal and seedling orchards in many countries (ELDRIDGE 1975). These clonal orchards were established mainly with grafts, although cuttings from young trees are being used increasingly with *E. grandis* to avoid graft incompatibility. For example BURGESS (1974) found that nearly all grafts failed within a year of planting although he had obtained over 80% take in the nursery. He and others have avoided graft incompatibility by developing techniques to strike roots from coppice shoots taken from the base of selected young trees (CHAPERON and QUILLET 1977). The use of tissue or organ culture is a possibility for future orchards (DE FOSSARD *et al.* 1974).

Open-pollinated seedlings from outstanding phenotypes are the basis of many other eucalypt orchards. The reports of FRANKLIN and MESKIMEN (1973, 1974) describe a eucalypt selection program in Florida which shows great promise without requiring very difficult techniques. 'A system of combined (between and within family) recurrent selection is being used with successive generations of open-pollinated families in *E. grandis, E. robusta* SM., *E. camaldulensis* and *E. tereticornis.* Seedling seed orchards are derived from each successive genetic base population by a system called "two-stage selection". The first stage involves selection of from 1 to 3 trees in each family which has acceptable trees. One year after first-stage roguing, seed is collected from all trees to produce progeny for the next generation genetic base population. If commercial seed is needed at this stage, it would be harvested from only a few of the best trees in the whole plantation. Following first-stage seed collection, second-stage roguing creates the commercial seed orchard composed of the best trees from 10 to 15 per cent of the original families' (FRANKLIN and MESKIMEN 1974).

It would be difficult to predict the results of trying the same method with other species in other places since the original Florida base populations were not a single good provenance of each species but several provenances with unequal numbers of selected trees from each. Thus the effects of selecting between and within provenances were confounded. Nevertheless the strategy of 'select and see what happens' was cheap and highly successful and must be considered for many eucalypt improvement programs.

Recommendations

For an effective long term program of genetic improvement of a eucalypt population —

1. Look carefully at the base population. Find out whether it is of the best species and best provenance, and whether it is likely to contain enough variability for continuous selection over several generations. If the base population is deficient, plan to expand it by seed collections in appropriate natural stands.
2. If there is little or no information on the basic genetic parameters of the species try to arrange for someone to find out the attributes of the breeding system and the levels of additive and non-additive variance for commercially-important characters of that particular species.
3. Then on the basis of knowledge of the population choose an appropriate method of producing improved seed. Clonal seed orchards are the best choice if the technical skills and money are available for grafts or cuttings. If there are difficulties with vegetative reproduction an open-pollinated seedling seed orchard, retaining the identity of families, is the next best. In any case seed production areas should be made in stands of suitable origin to provide an inexpensive supplement to more elaborate plans.
4. Plan for a future crossing program of controlled pollinations of selected trees, progeny testing and recurrent selection for continued genetic improvement over several generations.

Forest managers preparing to grow their own eucalypt seed have the opportunity to make considerable genetic improvement by several methods, few of which have been adequately tested. A compilation of the experience from research and practice rapidly accummulating in many countries would allow better management decisions to be made on the genetic improvement of eucalypt populations.

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Precocious Flowering of 2–3-year old Japanese Red Pine saplings at Dehra Dun

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Summary

Precocious flowering at only 2—3 years age of *Pinus densiflora* introduced at Dehra Dun, is reported. Similar early flowering records in this and other pines of the *Lariciones* group from other parts of the world, are briefly reviewed; and its value in breeding work indicated.

Key words: Precocious flowering; *Pinus densiflora* SIEB et ZUCC.; Japanese Red Pine.

Zusammenfassung

Bei eingetopften Kiefern *(Pinus densiflora* SIEB. et ZUCC.) konnten im 3. Jahr nach der Aussaat weibliche und männliche Blüten beobachtet werden.

Introduction

The temperate Japanese Red pine *(Pinus densiflora* SIEB. et ZUCC.), either by itself or in hybridization with other Pines, is of potential commercial importance in Japan, Korea and some parts of the U.S.A. (TODA, 1974; WRIGHT, 1976). As for India, earlier introductions indicate the suitability of this exotic species only for the higher temperate altitudes (above 2400 m.) of the Himalayas. It grows there much faster than the native Firs and hence could serve well for high altitude afforestation in the Firzone. At lower elevations, such as at Dehra Dun (640 m.), a few isolated old trees still surviving in local gardens show very poor form and extremely stunted growth. So it seems that this high latitude temperate species is not suited for subtropical conditions at Dehra Dun.

Material

Recently, a small seed sample of an unknown provenance from Japan had been received. Out of the 400 seeds initially sown of this lot in nursery beds at New Forest, Dehra Dun (30° 30' 40" N.Lat.) on 18th February, 1975, 138 seedlings had resulted. These had been pricked out on 12th March of the same year into polybag containers and transferred a year later into 22 cm wide earthen pots, and thus

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